

Plio-Pleistocene correlations between climatic change and evolution in terrestrial mammals: the 2.5 ma event in Africa and Europe

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Abstract. Climatic change has been a marked feature of the past five million years. Among several stepwise changes known from this time span, the onset of the first northern hemisphere glaciations at ca. 2.5 ma stands out as an event of particularly global impact. Any causal relationship between climatic and evolutionary changes should therefore be most apparent in its aftermath. A survey of the terrestrial mammal faunas of Africa and Europe from earlier Pliocene to Middle Pleistocene times indicates just such a relationship in patterns of lineage turnover and within-species changes.

Key words: Pliocene, Pleistocene, Africa, Europe, mammals, evolution, climate.

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I. INTRODUCTION

Throughout the Plio-Pleistocene there has been a trend towards lower temperatures interrupted by stepwise increases in cooling. This trend was eventually dominated by the orbitally-induced cyclical appearances of polar and higher altitude ice sheets of the Pleistocene ice ages (SHACKLETON & OPDYKE 1977; SHACKLETON et al 1984; PRENTICE & DENTON 1988).

It is now clear that one of the most important of these stepwise changes occurred at ca. 2.5 ma with the first major northern hemisphere glacial event of the Plio-Pleistocene (SHACKLETON et al. 1984). This period witnessed the beginnings of loess deposition in China (KUKLA 1987), increasing cold in the Andes (HOOGHIEMSTRA 1986), palynological, lithostratigraphic and cryoturbic indicators of cold in the Netherlands (DE JONG 1988) and the beginning of the classic Mediterranean seasonal pattern (ZAGWIJN & SUC 1984). In Africa the Sahara desert became a permanent phenomenon, the closed forest and woodlands of eastern Africa were transformed into savannas and western Africa was subjected to increasing aridification (VAN ZINDEREN BAKKER & MERCER 1986; BONNE-

FILLE & VINCENS 1985; BONNEFILLE et al. 1987; WESSELMAN 1984; JANECEK & RUDDIMAN 1987).

The inference of significant change in the vegetation in eastern Africa at this time has recently been questioned by CERLING (1992), based on an analysis of the stable carbon and oxygen isotopes of palaeosol carbonates. His results have led him to argue that significant opening of the vegetation, as indicated by increasingly positive $\delta^{13}\text{C}$ values indicative of enhanced proportions of C_4 grasses, are essentially earliest Pleistocene and later. However, two points should be made. First, the sites discussed by CERLING and cited as depleted in C_4 indicators until post 2.5 ma are almost entirely water margin localities, hardly open savannas and therefore areas where C_4 plants would surely have been relatively less frequent. It is therefore not evident that such localities record the wider vegetational picture of the time. The fact that such localities do record a more open pattern of vegetation by around 1.7 ma is itself a strong indication of a wider pattern of change that must have predated events at his chosen sites. Second, although CERLING himself makes the point that a continuous pattern of C_4 increase may be seen since the middle Miocene, his Figure 2 appears to show a distinct break towards more positive values in the slope of $\delta^{13}\text{C}$ at or about 2.5 ma.

The overall picture is therefore one of significant global change in the physical environment at ca. 2.5 ma. If there is any degree of congruence between the pattern of climatic change and events in the evolution of the terrestrial mammalian fauna, then this period and its immediate aftermath should provide some of the clearest evidence, as has been suggested (VRBA 1985a; TURNER & WOOD 1993b). In this paper I shall draw together some of the published data on later Pliocene mammalian faunal evolution in Africa and Europe, concentrating on the 2.5 ma event but also looking a little more widely at subsequent events in Europe where the nature of the evidence gives a rather less detailed picture.

II. EVOLUTIONARY CHANGES

Africa

Eastern Africa has one of the richest and best dated records of Plio-Pleistocene mammalian faunal change as a result of the interleaving of volcanic and fossiliferous sediments containing remains of some 150 larger species in the period between 4.0 ma and 1.0 ma (BROWN & FEIBEL 1991; FEIBEL et al. 1989; TURNER & WOOD 1993a). The rich assemblages have permitted extensive biostratigraphic correlations to be made with the important but undated southern African deposits of the Transvaal where some 80 larger species are recorded over the same period (VRBA 1982; DELSON 1984, 1988; TURNER & WOOD 1993a). Many detailed studies of the evolution of particular lineages have now been undertaken against this background. The results in the context of the present discussion may be summarised as follows.

Proboscidea: The species *Elephas recki* DIETRICH, 1915 displays a steeply rising trend through what have been called five time-successive sub-species towards higher tooth crowns with larger numbers of plates and thinner and more folded enamel over time (BEDEN 1983, 1985). The sequence is seen most clearly in the hypsodonty

indices of material from both Omo Shungura and the Koobi Fora Formation deposits east of Lake Turkana (Table I), although BEDEN unfortunately quoted ranges rather than means for his material. BEDEN saw this change as evidence of adaptation to tougher vegetation in more arid conditions based on comparisons with European mammoths, and emphasised the apparent acceleration in that evolution with the appearance of the *Elephas recki atavus* ARAMBOURG, 1947 morphotype in upper Member F and Member G at Shungura (ca. 2.3 ma). This change is in fact first seen as a major increase in the maximum value of the index during the lifespan of the subspecies *E. recki shungurensis*, and a marked increase in the range of morphometric variation, followed by a significant upward shift in the lower value between ca. 2.3 and 2.0 ma. It is possible that some of the increase in the range of the index began prior to 2.5 ma, but the most marked shifts do appear to post-date that time.

Table I

Elephas recki and *E. ekorensis* from Omo and Koobi Fora deposits. Hypsodonty index derived from maximum height and width of M3/. Koobi Fora stratigraphy refers to tuffs. Details from BEDEN (1983, 1985) and FEIBEL et al. (1991).

| Taxon | M3/Hypsodonty Index (range) | Omo | Koobi Fora Formation | Central Age (ma) |
|---------------------------|-----------------------------|------------|----------------------|------------------|
| <i>E. ekorensis</i> | 100-110 | Usno ‡ | | 3.3 |
| <i>E. r. brumpti</i> | 101-116 | A sup. - B | sub Tulu Bor | 3.0 |
| <i>E. r. shungurensis</i> | 118-138 | C-F | Tulu Bor-Burgi | 2.5 |
| <i>E. r. atavus</i> | 116-160 | F sup.- G | Upper Burgi | 2.3 |
| <i>E. r. ileretensis</i> | 137-172 | * | sub Okote | 1.9 |
| <i>E. r. recki</i> | 177-200 | K-L | above Okote | 1.5 |

‡ *E. ekorensis* also occurs at Kanapoi and in the Hadar Formation.

* The subspecies *ileretensis* is not certainly identified at Shungura.

These changes in *Elephas* between 2.3 and 2.0 ma are paralleled by the local disappearance of the genus *Loxodonta* CUVIER, 1825 in eastern Africa until the Upper Pleistocene. *Loxodonta*, a browser, had until that time undergone a similar trend towards greater hypsodonty, more plates and thinner and more folded enamel (BEDEN 1985), but its disappearance may have been linked to the local loss of humid woodlands.

According to BEDEN (1983), the probable ancestor of *E. recki* is *E. ekorensis* MAGLIO, 1970. Its teeth differ little from those of the earliest subspecies of *E. recki*, *E. r. brumpti*

BEDEN, 1980, although those of the latter do have somewhat thinner and more folded enamel and higher plates. However, as may be seen in Table I, the hypsodonty index range for *E. ekorensis* is little different from that of *E. r. brumpti*, and it is therefore apparent that the change in index seen within *E. recki* is indeed a new phenomenon, rather than the simple continuation of any earlier trend.

S u i d a e : Suids, which are abundant in eastern African deposits, exhibit marked morphometrical change over time. Despite the taxonomic confusion that has been a feature of discussions of African suids, it is clear that increases in hypsodonty are a major feature of those changes (TURNER & WOOD 1993b). *Notochoerus scotti* (LEAKEY, 1943), the common notochoere of the Turkana Basin in the period 3.0-2.0 ma (HARRIS et al. 1988), has larger, wider and taller teeth than other members of the genus, thinner and more crenulated enamel and a thicker cover of cementum (HARRIS 1983a). In the genera *Kolpochoerus* VAN HOEPEN & VAN HOEPEN, 1932 and *Metridiochoerus* (HOPWOOD, 1926) molar volume and total occlusal area increases abruptly at about the time that *Equus* LINNAEUS, 1758 first appears in the Omo Shungura Member G deposits at around 2.3 ma (see below), while the species *M. andrewsi* HOPWOOD, 1926 shows increased hypsodonty (Table II).

Table II

Hypsodonty Index for M3/ of *Metridiochoerus andrewsi* from Koobi Fora Formation deposits. Data from HARRIS (1983b)

| | Metridiochoerus andrewsi zone = KBS | <i>Notochoerus scotti</i> zone = upper Burgi |
|----------|--|---|
| Mean±SEM | 80.9±4.1 | 71.3±2.5 |
| Range | 54-103 | 61-83 |
| SD | 15.5 | 7.1 |
| N | 14 | 8 |

B o v i d a e : The Bovidae is the most taxonomically diverse of the large-mammal families in the African Plio-Pleistocene, and the one most often employed in discussions of environmental change. VRBA (1985a, 1985b, 1988) identified a major change in the composition of the bovid fauna of eastern Africa at around 2.5 ma, while GENTRY (1985) pointed out that alcelaphines, marked by hypsodont teeth and strongly cursorial adaptations, only become common in the Shungura deposits in Members F and G and onwards. Something of this pattern is summarised in Table III, where significant first appearances of some bovid taxa are given. The overall pattern indicates a staggered response to changed conditions at around 2.5 ma damped by the effects of refugium-like conditions in areas where water was available (VRBA 1988). Thus the upper Burgi Member of the Koobi Fora

Table III

Bovid first records close to 2.5 ma Sources VRBA (1985b, 1985c, 1988), HARRIS (1991a), GENTRY (1985), HARRIS et al. (1988)

| Taxon | Locality |
|---------------------------------|--|
| <i>Gazella praethomsoni</i> | Shungura F |
| <i>Antilope sub torta</i> | Shungura C (Immigrant) |
| <i>Antidorcas recki</i> * | Shungura F |
| <i>Oryx</i> sp. | WT Upper Lomekwi, ET KBS |
| | ? Shungura C (Immigrant) |
| <i>Megalotragus kattwinkeli</i> | Shungura B10 (cf), G and Sterkfontein 4 |
| <i>Pelorovis</i> sp. @ | Shungura D, F, G |
| <i>Tragelaphus strepsiceros</i> | Shungura G |
| <i>Tragelaphus gaudryi</i> | Shungura E |
| <i>Tragelaphus scriptus</i> | WT Lower and Upper Lomekwi, Kaitio |
| <i>Tragelaphus pricei</i> | Makapansgat 3, Shungura C |
| <i>Kobus ellipsiprymnus</i> | Shungura G |
| <i>Menelikia lyrocera</i> | WT Lokalalei |
| <i>Menelikia</i> sp. (?) | WT Upper Lomekwi |
| <i>Ovibovini</i> sp. | Shungura C, D and G |
| <i>Parmularius braini</i> | Makapansgat 3, Shungura C |
| <i>Damaliscus</i> sp. | WT Lower and Upper Lomekwi |
| <i>Connochaetes</i> sp. | WT Upper Lomekwi, Shungura G, ET Upper Burgi, Sterkfontein 4 |
| <i>Beatragus antiquus</i> | Shungura G |
| <i>Aepyceros melampus</i> | WT Kalochoro, Shungura G, ET Upper Burgi |
| <i>Hippotragus</i> sp. | Shungura G |

VRBA (1988) disagrees with allocations of GENTRY (1985a) in Shungura B10 (*), B10 and C @.

Formation has a predominance of wet grassland-loving reduncines, but dry grassland adapted alcelaphines are more common than woodland taxa such as tragelaphines (FEIBEL et al., 1991) and indicative of wider habitat changes (Table IV).

In addition to these changes in faunal structure at the tribal level, there is also a shift in emphasis to molars at the expense of premolars in later species of lineages (Table IV). This shift is apparent in the Alcelaphini, particularly in the genera *Megalotragus* VAN HOEPEN, 1932, *Connochaetes* LICHTENSTEIN, 1814, *Beatragus* HELLER, 1912 and (in some cases) *Parmularius* HOPWOOD, 1934, and often involves the loss of the lower second premolar and the reduction of the third premolar to a peg-like structure (VRBA 1984; HARRIS 1991a). This emphasis on the molar tooththrow seems to indicate increasing adaptation towards coping with open, dry grasslands.

Table IV

Summary of major developments in eastern African Bovidae in the period 2.5-2.0 ma. See text

| Turnover | Tribal Compositions | Dental Adaptations |
|---|---|--|
| ca. 20 new taxa (including immigrants) in the period 2.5-2.0 ma | Wet grassland-loving reduncines predominate in Koobi Fora Upper Burgi Member around 2.3 ma, but dry grassland-adapted alcelaphines more common than woodland tragelaphines. Alcelaphines become more common in Omo Shungura F and G onwards | Later species in lineages show emphasis on molars, decrease in premolars: especially seen in Alcelaphini |

E q u i d a e : At around 2.3 ma a dispersal from an ultimate centre in the New World brought the genus *Equus* into Africa via Eurasia (LINDSAY et al. 1980; AZZAROLI et al. 1988), where it gradually replaced *Hipparion* DE CRISTOL, 1832. The new genus is first recorded in the Upper Burgi Member at East Turkana, the Kalochoro Member at West Turkana and Member G of the Shungura sequence, and may have been represented by more than one species (EISENMANN 1983; HARRIS et al. 1988).

Hypsodonty in *Equus* is generally considered to be an adaptation to consumption of silica-rich fodder (EISENMANN 1983). Although *Equus* does not appear to have become more hypsodont once it appears in Africa, hypsodonty in *Hipparion* increased through the Shungura Formation, with an observed range of 256-313 for an index of height/anteroposterior diameter of upper molars in Shungura B and C and 291-370 in Shungura F and G (EISENMANN 1983). Both genera are therefore recording the same change in the physical environment and subsequent changes in vegetation, one by its incursion and the other by its renewed dental adaptations.

R h i n o c e r o t i d a e : The two extant African genera *Ceratotherium* GRAY, 1867 (the white rhino) and *Diceros* GRAY, 1821 (the black rhino) are known from the mid-Pliocene. There is evidence of an increase in hypsodonty in the lineages (HARRIS 1983b), especially at around 2.0 ma in the case of *C. simum* (BURCHELL, 1817) from the Shungura deposits, together with signs of a progressive elongation of the skull of *Ceratotherium*, an apparent adaptation towards consumption of grass below a preferred height of 10 cm.

H i p p o p o t a m i d a e : The replacement of the genus *Hexaprotodon* FALCONER & CAUTLEY, 1836 by the extant *Hippopotamus* LINNAEUS, 1758 (GÈZE 1985; HARRIS 1991b) that begins in the upper Burgi member at Koobi Fora around 2.3 ma indicates a greater reliance on an aquatic environment. HARRIS (1991b) suggests that increasing aridity would have threatened the hexaprotodonts, with their preference for more widely distributed grass pastures and woodlands, and increased the advantage of exploiting the remaining bodies of water. Attempts by the hexaprotodonts to respond to this pressure may inferred from the fact that advanced specimens of *Hexaprotodon karumensis* CORYNDON, 1977 also display more elevated orbits, indicative of a more aquatic lifestyle, while retaining terrestrial adaptations of the postcranial skeleton. There is also evidence of an increase in the enamel thickness of their brachydont teeth over time (HARRIS 1991b: 37),

a possible effect of changes in fodder, while *Hippopotamus* displays hypsodont teeth from the outset.

Carnivora: Changes in the composition of the order in Africa over the past several million years must in part reflect changing conditions, although it is to be expected that members of the order would be less tied to immediate circumstances than ungulates dependent on vegetation (TURNER 1990). The genus *Canis* LINNAEUS, 1758, represented by several species of jackal, first appears there at ca. 2.5 ma, most probably through dispersion from Eurasia where it also becomes more common. Such animals scavenge from the kills of larger predators in relatively open terrain.

The extant larger predators, such as *Panthera leo* (LINNAEUS, 1758), *Panthera pardus* (LINNAEUS, 1758), *Acinonyx jubatus* (SCHREBER, 1775) and *Crocota crocota* (ERXLEBEN, 1777) are known in Africa for close to 4.0 ma (TURNER 1990), and their appearances are not obviously correlated with any particular environmental events or perturbations. Indeed, the precise origins in time and space of most of the larger carnivores remain obscure. By 1.5 ma two species of machairodont cat, *Homotherium latidens* (OWEN, 1846) and *Megantereon cultridens* (CUVIER, 1824), plus the 'false' machairodonts *Dinofelis barlowi* (BROOM, 1937) and *D. piveteaui* (EWER, 1955) and the hyaenid genus *Chasmaporthetes* (HAY, 1921), had become extinct in the continent (TURNER 1990: Table 1). Those extinctions were significant events within the history of the guild, the other side of the evolutionary coin from speciation, and as such are most reasonably connected with earlier changes in the ungulate fauna, the vegetation and, ultimately, the climate.

Cercopithecidae: Significant changes occur in this family. The large baboon, *Theropithecus brumpti* (ARAMBOURG, 1947), thought to have occupied gallery forest (ECK & JABLONSKI 1987), became extinct during the period between 2.5 and 2.0 Ma, to be replaced from around 2.5 ma by *T. oswaldi* (ANDREWS, 1916). That this change may reflect the shift to more open habitats is strongly implied by the fact that the latter species is well-known in southern Africa at the Lower Pleistocene hominid sites of the Sterkfontein Valley in what appear to have been open conditions (DELSON 1988; VRBA 1988). During its appearance, *Theropithecus oswaldi* exhibited several dental trends (LEAKEY 1976), including an increase in the size and complexity of its molars, a reduction in muzzle length and an increase in the height of the ascending ramus of the mandible.

Within the family as a whole, DELSON (1984, 1985, 1988) has suggested a turnover in the composition of cercopithecoid assemblages between 2.5 and 2.0 ma. His African cercopithecoid zones 4 and 5 (DELSON 1988: Fig. 21.2) record respectively the initial co-occurrence of Pliocene taxa alongside their Pleistocene replacements and then, by 2.0 ma, the appearance of largely modern forms.

Hominidae: The 'robust' australopithecine genus *Paranthropus* (BROOM, 1938) appears to date from as early as 2.6 ma, based on specimens from Omo Shungura deposits (BROWN & FEIBEL 1988; WALKER, et al. 1986). But according to HOWELL et al. (1987) and SUWA (1988), specimens from below Shungura G lack derived features seen in the dentition of *P. boisei* (LEAKEY, 1959) (*sensu stricto*), especially the extreme talonid expansion of the P₄s (SUWA 1988: Fig. 13.7), implying a shift towards the extremes of paranthropine development by the time the Member G deposit was forming.

Homo rudolfensis ALEXEEV, 1986, based on material from Koobi Fora (WOOD 1991, 1992) has an enlarged neurocranium and *Homo*-like endocranial morphology while its facial and dental anatomy most closely resembles *Paranthropus* (WOOD 1991). In particular, it has a large mandibular corpus, molarised roots and crowns of the mandibular premolars and a more orthognathic positioning of the face. The lower third molars appear to have been larger than the second molars, and the upper molars are larger than those of *A. africanus* DART, 1925. The tooth enamel of KNM-ER 1483 and 1802 is thicker than that of any other measured teeth allocated to early *Homo*. These features parallel those of *Paranthropus* previously linked to the consumption of tougher food items by studies of occlusal wear (GRINE 1981), and suggest a generalised response on the part of some of the hominids (TURNER & WOOD 1993b). The origins of the genus *Homo* remain unclear, but a cranial fragment from Baringo dated to 2.4 ma (HILL et al. 1992) together with teeth from Shungura deposits in the time range 2.1-2.4 ma (GRINE 1984) and a tentatively attributed cranial fragment from West Turkana deposits in the age range 1.9-2.35 ma may together be interpreted as strongly suggestive of appearance prior to 2.0 ma. Whether or not all, or indeed any, of these specimens can be referred to *H. rudolfensis*, it would appear that some burst of speciation and perhaps increased diversity took place within the Hominidae during the period of relevance to this discussion.

Europe

In the absence of the well-dated and at times lengthy sequences that characterise the Plio-Pleistocene deposits of eastern Africa, the history of the Eurasian mammal fauna has to be reconstructed from a large number of discrete localities where dating itself often depends on correlation. The result is a rather broader picture of faunal history, albeit based on numerous sites and deposits, without the more finely detailed patterns of morphometrical change that characterise the study of some African lineages in the later Pliocene and earlier Pleistocene. Nevertheless, some points stand out as turnover events in the fauna (TORRE 1987; TORRE et al. 1992; MASINI & TORRE 1990; AZZAROLI et al. 1988; SALA et al. 1992; TURNER 1992a, 1992b; AGUSTI & MOYA-SOLA 1992).

A succession of authors (KURTÉN 1963, 1968; MAGLIO 1975; AZZAROLI et al. 1988; AGUIRRE & MORALES 1990) have stressed the major turnover in European mammalian faunas that occurs at the end of the Villafranchian faunal span. However, the time around 2.5 ma still emerges as a significant point in faunal evolution, with the first appearances of *Equus*, *Mammuthus meridionalis* (NESTI, 1885) and the cervid genus *Eucladoceros* FALCONER, 1868, and the disappearance of *Mammuthus* BLUMENBACH, 1799 and *Tapirus* BRISSON, 1862. AZZAROLI et al. (1988) argue for a more open, parkland and savanna landscape at this time, based on assemblages from a diversity of localities.

Although the European record cannot provide the detailed resolution of evolution in faunal elements in the immediate aftermath of the 2.5 ma event that is possible for Africa, it seems apparent that trends set in motion there by the step-like transition in climatic parameters at 2.5 ma have their own longer term pattern. The dominant conditions of the Pleistocene have been colder than the present day, with increasing aridity, and the interglacial periods like the one we are now in have been relatively short-lived (TURNER 1992a). The effect of this long-term emphasis on colder and drier climates culminates in

the typical glacial faunas seen in the latter part of the Middle Pleistocene in Europe, so that there is clearly a role for climate in the evolution of the European fauna. The appearance of ever more modern ungulates during the later Pliocene and earliest Pleistocene is paralleled at the beginning of the Pleistocene by the local disappearance of the hyaenid species *Chasmaporthetes lunensis* (DEL CAMPANA, 1914) and *Pliocrocota perrieri* (CROIZET & JOBERT, 1828) (although the latter re-immigrates during the Middle Pleistocene) and followed by the local extinction of the machairodont cat *Megantereon cultridens* (TURNER 1992a: Tables 1-4). These extinctions resemble some of those seen at a similar time in the African large carnivore guild, although crucial differences such as the continued existence of *Homotherium latidens* and the much later appearance in Europe of modern taxa such as *Panthera leo*, *Panthera pardus* and *Crocota crocuta* serve to remind us that the details of response differ according to initial regional conditions and local circumstances.

So far as individual lineages are concerned, some of the best evidence for environmentally-directed change comes, as it does in Africa, from the Elephantidae, with the gradual increase in hypsodonty and lamellar frequencies seen in the various, time successive species of *Mammuthus* (BROOKES, 1828) following the first appearance of the genus in Eurasia at the time of the 2.5 ma event (LISTER, 1993). In many ways, this evolution in dental characters is similar to that undergone by *Elephas recki* in Africa, except that in the Eurasian case the morphological trend has been traditionally interpreted as evidence for three chronospecies, *Mammuthus meridionalis*, *M. trogontherii* (POHLIG, 1889) and *M. primigenius* (BLUMENBACH, 1799), instead of subspecies. The greatest change occurs over the time span from around 1.6 ma to 0.6 ma, and within *M. meridionalis* and between that taxon and *M. trogontherii*, with a change in the index of hypsodonty for the M3/ from 116 to 194 (derived by interpolation from Figure 2 of LISTER, 1993). LISTER's data also make one other interesting point, in that after about 0.5 ma there appears to be no further increase in the index of hypsodonty, but the lamellar frequency continues to increase somewhat before reaching a stable point. It would seem that at about 200, the figure attained by *Elephas recki* in Members K and L at Shungura, the limit of hypsodonty had been reached and the only possible further adaptation to continued cold-climate vegetation was in lamellar frequency.

III. DISCUSSION

Diverse lines of evidence point to a significant global climatic cooling event at ca. 2.5 ma and a worldwide vegetational response. In the ensuing 0.5 ma in Africa the larger mammal fauna exhibits a shift towards grassland species, while many lineages underwent independent adaptations towards coping with a diet of tougher and perhaps more abrasive foodstuffs. Lineage turnover, particularly in bovids, equids and hippos, is thus matched by increases in hypsodonty in pigs, elephants and the equid genus *Hipparion*, together with an increased emphasis on the molar dentition in the Alcelaphini. Changes in the primates include lineage turnover in the Cercopithecidae, the emergence of our own genus, *Homo*, and a number of parallels in masticatory developments in *Homo*, *Paranthropus* and *Theropithecus*. These changes are summarised in Table V.

Table V

Summary of evolutionary events in various African mammalian groups in the period 2.5-2.0 ma. For details see text

| Taxon | Events |
|-----------------|---|
| Hominidae | <i>Paranthropus</i> and <i>Homo</i> : hypermasticatory trend: origins of <i>Homo</i> and marked diversity |
| Cercopithecidae | Significant lineage turnover; <i>Theropithecus brumpti</i> replaced by <i>T. oswaldi</i> , in which subsequent masticatory developments parallel those seen in the Hominidae |
| Carnivora | Incursion of <i>Canis</i> , eventual extinction of machairodonts and continued success of pantherine cats points to effects of change to open country and more cursorial prey |
| Deinotheriidae | Gradual extinction |
| Elephantidae | Very significant increase in hypsodonty, plate numbers and enamel folding in <i>Elephas recki</i> with sequence of subspecies: local disappearance of <i>Loxodonta</i> |
| Equidae | Incursion of <i>Equus</i> from Eurasia: increased hypsodonty in <i>Hipparion</i> during subsequent period of overlap |
| Rhinocerotidae | Increased hypsodonty and grazing adaptations in skull of <i>Ceratotherium</i> |
| Suidae | Increased hypsodonty and tooth volume in <i>Kolpochoerus</i> and <i>Metridiochoerus</i> |
| Hippopotamidae | Lineage turnover, with rise to dominance of <i>Hippopotamus</i> , and emphasis on aquatic lifestyle in both that genus and <i>Hexaprotodon</i> |
| Giraffidae | No evident change |
| Camelidae | No evident change |
| Bovidae | Massive lineage turnover, including immigrations; change in the broad tribal composition of assemblages, with more open country species; dental adaptations to grazing |

In Europe, a similar shift to a more open-country fauna is also seen, together with a longer term pattern of change in faunal composition and evolution within lineages adapting to predominantly colder and more arid conditions. The parallels between African and Eurasian Elephantidae, albeit over longer timescales, are particularly noteworthy. Not discussed here, but of direct relevance to this discussion, is the fact that a similar pattern of change seems to occur in the larger mammalian fauna of the Yushe Basin of Shanxi Province in northern China at around 2.5 ma (FLYNN et al. 1991), where extinctions in particular are strongly evident.

Most recently, FOLEY (1993, 1994) has sought to argue that evolutionary events in African hominids and cercopithecids in particular are not closely related to climatic change, concluding that no such overall correlations can be demonstrated, with some possible exceptions in the case of cercopithecoid extinctions and speciation in the Bovidae. Instead, he has invoked notions of community co-evolution as a generalised model, albeit with some influence of climatic change mediated through competition. However, the model of

climatically-induced change tested by him considers appearance and extinction of terrestrial primate taxa over virtually the whole timespan of the Hominidae, and sets these events against the oscillations of climate inferred from the deep-sea core record rather than against stepped transitions in climate. Such a test appears unsuited to dealing with the problem of inferring causation. The uncertainties of dating and of allocation of events to one or other time period will surely affect any calculation, while the small number of taxa over the timespan makes it difficult to see how correlations could realistically be assessed. Moreover, the test omits consideration of within-taxon responses to climatic and habitat changes of the kind discussed here, as exemplified in the species *Elephas recki*, responses which, when taken together with turnover events, provide a much greater basis for interpreting the patterns over large and diverse sections of the fauna (TURNER & WOOD 1993b). In any event, unless we are to expect a high rate of evolutionary turnover in taxa, it would seem likely that if speciations and extinctions do correlate with environmental events then they will do so with significant steps in climatic change, rather than with every feature of what were in many ways short-term oscillations. Such oscillations are likely to induce similar short-term oscillations in distributions rather than a revolution.

The universal nature of the changes in the African terrestrial fauna outlined here argues strongly against their being dismissed as taphonomic artefacts, while the similarity in the timing and patterning observed across clades suggests that all were in response to an external, physical agency and not what VRBA (1985a: 231) referred to as the 'weak environmentalism' of concepts such as interspecific competition, dispersal and radiation into "available niches". While it is undoubtedly true that correlation alone, although suggestive, does not necessarily indicate causation (WHITE 1985), there would seem to be a point at which a non-acknowledgement of the implications of mounting evidence for correlations between a number of diverse events and a known shift in conditions likely to provoke such events becomes perverse.

That said, it remains clear from the foregoing discussion that the idea of a faunal "event" in the fossil record at 2.5 ma, somehow precisely correlating with climatic shifts, is a somewhat misplaced expectation. It would be far more reasonable to expect some kind of series of events following a major climatic step, as the vegetation changed first of all and provoked a reaction among the ungulates dependant on it and thus, eventually, among the larger carnivores. Only if the effect at each stage was sufficiently marked would it be felt further down the chain. In that limited sense it is true that there is no faunal event at 2.5 ma in Africa because, as in Europe, most of the effects of climatic change are to be seen in the period that follows.

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